# *On Some Features in the Hereditary Transmission of the Albino Character and the Black Piebald Coat in Rats.*—Paper II.

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(Communicated by Professor A. D. Waller, F.R.S. Received January 14,—Read May 21, 1908.)

This paper contains a further record of experiments which were begun at the same time as those recorded in my first paper.* The method of interpreting results in the present paper is the same as that used in the first one, and is based upon the same working hypothesis, *i.e.*, Bateson and Punnett's "Presence and Absence" hypothesis and Cuénot's theory of colour. The cost of these experiments has been defrayed by a grant from the Government Grant Committee of the Royal Society.

## The Experimental Matings.

### (1) (a) *Cr* 4 × *Cr* 4 = *Albino* × *Albino.*

Twenty pairs of albinoes were mated. There was a total offspring of 174 individuals, all albinoes. Some of these albinoes had a near albino ancestry, while others had a pigmented one. The details of the ancestry may be seen upon reference to the Table of Ancestry, pp. 390—391.

### (b) "*Ghost*" *or Zygotic Patterns in Albinoes.*

I have already, in the first paper, given an account of the "ghost" pattern as shown in the offspring of one mating (experiment 74). I have now to describe a second case. In experiment 19A there was a total offspring of 15, in two litters of six and nine individuals. The first litter was at a much earlier date than the second, and I did not pay any particular attention to the appearance of the coat in the individuals of this litter. By the time the second litter was born, I had discovered the existence of the "ghost" pattern in albinoes. It is possible, therefore, that the first litter showed it, but since it is only a transitory matter of a few weeks, it will be unobserved unless looked for at the particular period at which it appears. Of the nine albinoes born in the second litter, two died quite young, and the remaining seven all

* "On Some Features in the Hereditary Transmission of the Self-black and the "Irish" Coat Character in Rats.—Part I," 'Roy. Soc. Proc.,' B, vol. 80, 1908.

showed the "ghost" of the self-pattern. One of these "self-ghost" individuals was mated with a Cr 5 (see experiment 37C)* and gave a coloured offspring, all of the self-pattern. The young consisted of nineteen "Irish" *b* individuals, obtained in three litters. Since the self-pattern is dominant to the piebald, it is clear that the pigmented piebald parent (Cr 5) could not have been carrying the self-pattern determiner. The albino parent is therefore the only source through which it could have come. And it should be noticed that one of its G-Ps. (experiment 74), and three of its G-G-Ps. (experiments 71 and 66A) had the self-pattern coat.

Now, on the basis of gametic purity and segregation, it is expected that one-half of the 15 offspring in experiment 19A of which the albino parent described above was one will carry the self-pattern determiner. By an ocular demonstration, corroborated by a subsequent breeding test, the expectation is thus shown to be fulfilled.

(2) *Cr* 4 × *Cr* 5 = *Albino* × *Piebald Black-White.*

(a) *Heterozygous Piebald* × *Albino.*

*Experiments* 29, 30, 31, 33, 34, 36, 37 *and* 37A.

The expectation in this cross is 1 Cr 4 : 1 Cr 5. The result is 44 Cr 4 + 55 Cr 5. The high proportion of the Cr 5 type is due to mating No. 30 (p. 391). If this is eliminated, the figures are 32 Cr 4 + 33 Cr 5. The disturbance of the proportions is due to the last two litters of this mating. They are:—

| | | | | | |
|---|---|---|---|---|---|
| 1st litter | = | 3 Cr 4 | + | 4 Cr 5 | |
| 2nd „ | = | 4 „ | + | 4 „ | |
| 3rd „ | = | 2 „ | + | 8 „ | |
| 4th „ | = | 3 „ | + | 6 „ | |

In experiment 34, one of the four albino offspring showed the piebald "ghost" pattern in its coat.

(b) *Homozygous Piebald* × *Cr* 4.

*Experiment* 32.

The expectation is that all the offspring shall be Cr 5. The result is 14 Cr 5.

(c) *Piebald* × *Cr* 4 *of more Complex Constitution.*

*Experiments* 35, 37B, *and* 37C.

In these crosses the result will depend upon the nature of the albino parent. If it be of cgBSsP constitution and the Cr 5 parent carries c recessive,

* See also Pedigree Chart 1, in first paper.

TABLE OF ANCESTRY AND OFFSPRING.

The symbols and abbreviations have the same signification as the corresponding ones in the first paper, *loc. cit.*

| Expt. | G–G–G–P. | G–G–P. | G–parents. | Parents. | Offspring. Cr 1. | Cr 2. | Cr 3. | Cr 4. | Cr 5. | Cr 6. "b." | Cr 6. "a." | Cr 7. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | See Expt.— | See Expt.— | See Expt.— | | | | | | | | | |
| 1 | — | — | — | Cr 4 ♂ 1 | — | — | — | 13 | — | — | — | — |
| | — | — | — | Cr 4 ♀ 2 | | | | | | | | |
| 2 | — | — | — | Cr 4 ♂ ? | — | — | — | 3 | — | — | — | — |
| | — | — | — | Cr 4 ♀ 151 | | | | | | | | |
| 3 | — | — | — | Cr 4 ♂ 150 | — | — | — | 7 | — | — | — | — |
| | — | — | — | Cr 4 ♀ 151 | | | | | | | | |
| 4 | — | — | — | Cr 4 ♂ 300 | — | — | — | 12 | — | — | — | — |
| | — | — | — | Cr 4 ♀ 301 | | | | | | | | |
| 5 | — | — | — | Cr 4 ♂ 400 | — | — | — | 24 | — | — | — | — |
| | — | — | — | Cr 4 ♀ 401 | | | | | | | | |
| 6 | — | — | — | Cr 4 ♂ 100 | — | — | — | 4 | — | — | — | — |
| | — | — | — | Cr 4 ♀ 101 | | | | | | | | |
| 7 | — | — | 3 | Cr 4 ♂ 153 | — | — | — | 11 | — | — | — | — |
| | — | — | 3 | Cr 4 ♀ 154 | | | | | | | | |
| 8 | — | — | 25 | Cr 4 ♂ 256 | — | — | — | 8 | — | — | — | — |
| | — | — | 25 | Cr 4 ♀ 257 | | | | | | | | |
| 9 | — | — | 1 | Cr 4 ♂ 8 | — | — | — | 15 | — | — | — | — |
| | — | — | 25 | Cr 4 ♀ 258 | | | | | | | | |
| 10 | — | — | 1 | Cr 4 ♂ 9 | — | — | — | 8 | — | — | — | — |
| | — | — | 1 | Cr 4 ♀ 10 | | | | | | | | |
| 11 | — | — | 1 | Cr 4 ♂ 11 | — | — | — | 7 | — | — | — | — |
| | — | — | 1 | Cr 4 ♀ 12 | | | | | | | | |
| 12 | — | — | 1 | Cr 4 ♂ 13 | — | — | — | 15 | — | — | — | — |
| | — | — | 1 | Cr 4 ♀ 14 | | | | | | | | |
| 13 | — | — | 1 | Cr 4 ♂ 15 | — | — | — | 5 | — | — | — | — |
| | — | — | 1 | Cr 4 ♀ 2 | | | | | | | | |
| 14 | — | — | 3 | Cr 4 ♂ 155 | — | — | — | 3 | — | — | — | — |
| | — | — | 3 | Cr 4 ♀ 156 | | | | | | | | |
| 15 | — | — | 5 | Cr 4 ♂ 405 | — | — | — | 7 | — | — | — | — |
| | — | — | 5 | Cr 4 ♀ 404 | | | | | | | | |
| 16 | — | — | 5 | Cr 4 ♂ 408 | — | — | — | 6 | — | — | — | — |
| | — | — | 5 | Cr 4 ♀ 407 | | | | | | | | |
| 17 | — | — | 25 | Cr 4 ♂ 263 | — | — | — | 3 | — | — | — | — |
| | — | — | 25 | Cr 4 ♀ 264 | | | | | | | | |
| 18 | — | — | 25 | Cr 4 ♂ 272 | — | — | — | 3 | — | — | — | — |
| | — | — | 25 | Cr 4 ♀ 273 | | | | | | | | |
| 19 | — | 47 and 5 | 61 | Cr 4 ♂ (1)(4)750/150/403 | — | — | — | 5 | — | — | — | — |
| | — | 47 and 5 | 61 | Cr 4 ♀ (2)(4)750/150/403 | | | | | | | | |
| 19A | 5, 23, and 48 | 71 and 66A | 74 | Cr 4 ♂ (2)(5)52/53/(3)(2)450/6/408 | — | — | — | 15[1] | — | — | — | — |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25 | — | — | — | Cr 5 ♂ 250 | — | — | — | 7 | 17 | — | — | — |
| | — | — | — | Cr 5 ♀ 251 | | | | | | | | |
| 26 | — | — | 25 | Cr 5 ♂ [2] 252 | — | — | — | — | 8 | — | — | — |
| | — | — | 25 | Cr 5 ♀ 253 | | | | | | | | |
| 27 | — | — | 25 | Cr 5 ♂ 260 | — | — | — | 3 | 4 | — | — | — |
| | — | — | 25 | Cr 5 ♀ 259 | | | | | | | | |
| 28 | — | 47 and 25 | 59 | Cr 5 ♂ (5)(9)750/152/252 | — | — | — | — | 3 | — | — | — |
| | 48, 25, and 3 | 62 and 20 | 38 | Cr 5 ♀ [3] (1)(1)1000/263/(2)55/(4)153/154 | | | | | | | | |
| 28A | 23 and 5 | 71 | 34 | Cr 5 ♂ (2)(4)(2)450/6/408/(5)(2)450/6/408 | — | — | — | 6 | 13 | — | — | — |
| | 23 and 5 | 71 | 34 | Cr 5 ♀ (1)(4)(2)450/6/408/(5)(2)450/6/408 | | | | | | | | |
| 29 | — | — | 25 | Cr 5 ♂ 252 | — | — | — | 8 | 10 | — | — | — |
| | — | — | 25 | Cr 4 ♀ 256 | | | | | | | | |
| 30 | — | — | — | Cr 5 ♂ 250 | — | — | — | 12 | 22 | — | — | — |
| | — | 3 | 14 | Cr 4 ♀ (3)155/156 | | | | | | | | |
| 31 | — | — | 26 | Cr 5 ♂ (4)252/253 | — | — | — | 5 | 3 | — | — | — |
| | — | — | 1 | Cr 4 ♀ 11 | | | | | | | | |
| 32 | — | — | 25 | Cr 5 ♀ 255 | — | — | — | — | 14 | — | — | — |
| | — | — | 3 | Cr 4 ♂ 156 | | | | | | | | |
| 33 | — | — | 25 | Cr 5 ♂ 261 | — | — | — | 5 | 5 | — | — | — |
| | — | 3 | 7 | Cr 4 ♀ (1)153/154 | | | | | | | | |
| 34 | — | 23 and 5 | 71 | Cr 5 ♂ (4)(2)450/6/408 | — | — | — | 4[4] | 4 | — | — | — |
| | — | 23 | 71 | Cr 4 ♀ (5)(2)450/6/408 | | | | | | | | |
| 35 | — | — | 25 | Cr 5 ♂ 262 | — | — | — | 8 | 3 | 2 | — | — |
| | — | — | 1 | Cr 4 ♀ 17 | | | | | | | | |
| 36 | — | — | 25 | Cr 5 ♂ 268 | — | — | — | 5 | 6 | — | — | — |
| | — | 1 | 13 | Cr 4 ♀ (1)2/15 | | | | | | | | |
| 37 | — | — | 25 | Cr 5 ♂ 266 | — | — | — | 2 | —[5] | — | — | — |
| | — | — | 1 | Cr 4 ♀ 19 | | | | | | | | |
| 37A | — | 47 | 59 | Cr 5 ♀ (3)(9)750/152/252 | — | — | — | 3 | 5 | — | — | — |
| | — | 47 | 57 | Cr 4 ♂ (2)(7)750/152/266 | | | | | | | | |
| 37B | — | 20 | 38 | Cr 5 ♀ (1)(1)1000/263/(2)55/(4)/153/154 | — | 2 | — | 3 | — | 1 | — | — |
| | — | 23 | 71 | Cr 4 ♂ (2)(2)450/6/408 | | | | | | | | |
| 37C | 38, 59, and 25[6] | 28 and 38 | 59A | Cr 5 ♂ [7] | — | — | — | — | — | 19[10] | — | — |
| | 71 and 66A[3] | 74 | 19A | Cr 4 ♀ [9] | | | | | | | | |

[1] Seven of these carried the self "ghost" pattern in their coats; and probably others carried some pattern too.

[2] One of these parents carried albinism recessive, for experiment 31 shows that some of their offspring carried albinism, and experiment 56 that some of them were pure.

[3] Experiment 37B shows that this individual carried albinism recessive.

[4] One of the four albinoes carried the piebald "ghost" pattern in its coat.

[5] The remainder of this litter was probably eaten.

[6] For G–G–G–G–P, see experiment 47.

[7] The number is: (3)(7)(1)1000/263/(2)55/(4)153/154/(1)(5)(9)750/152/252/(1)(1)1000/263/(2)55/(4)153/154.

[8] For G–G–G–G–P, see experiments 5, 23, and 48.

[9] The number is: (1)(2)(5)52/53/(3)(2)450/(6)408/(3)(5)52/53(3)(2)450/6/408. This albino carried the self "ghost" pattern in its coat. Hence the self-pattern in its offspring.

[10] There were four others, pigmented and self-pattern, but they died too early to determine whether they were Cr 6 "*a*," Cr 6 "*b*," or Cr 7.

the expectation is 2 Cr 4+1 Cr 5+1 Cr 6 *b*. The result (experiment 35) is 8 Cr 4+3 Cr 5+2 Cr 6 *b*.

If the albino parent be cgBSP and the Cr 5 parent is homozygous, the expectation is that the offspring shall be all of the "Irish" *b* form. The result (experiment 37c) is nineteen "Irish" *b* individuals.

If the albino* is cGgBSP and the piebald carries c recessive, the expectation is

2 Cr 4+1 Cr 2+1 Cr 6 *b*;

the result is 3 „ +2 „ +1 „ (experiment 37B.)

A sister of this albino parent (experiment 37B) was also mated with a black piebald (experiment 34). No grey individuals appeared in her offspring of eight. This, of course, is evidence that segregation of characters, *i.e.* blackness and greyness, occurred.

(3) *Cr* 5 × Cr 5 = *Black Piebald* × *Black Piebald.*

(a) *Heterozygous Cr* 5 × *Heterozygous Cr* 5.

*Experiments* 25, 27, *and* 28A.

The heterozygous Cr 5 carries c. The expectation is 1 Cr 4 : 3 Cr 5. The actual result is 16 Cr 4+34 Cr 5.

If we add the results of other observers, the figures stand thus :—

| | | | |
|---|---|---|---|
| † Crampe ..... | 12 Cr 4 | +45 Cr 5 | |
| ‡ Doncaster ..... | 4 „ | + 9 „ | |
| Mudge ..... | 16 „ | +34 „ | |
| Total ..... | 32 „ | +88 „ | = 1 : 3 nearly. |

With this total of 120 the predicted proportions are 30 : 90.

(b) *Heterozygous Piebald* × *Homozygous Piebald.*

*Experiments* 26 *and* 28.

The expectation in this case is that all the offspring will be piebald. The result is 11 piebalds. The further expectation is that some of the piebald offspring will be homozygous and some heterozygous. Experiments 31 and 56§ show respectively that the offspring of mating 26 was: one of them heterozygous and another homozygous.

* The previous behaviour of this albino is worth noticing (see experiment 45, first paper).

† 'Land. Jahr.,' vol. 14, 1885, pp. 596 and 597.

‡ 'Camb. Phil. Soc. Proc.,' vol. 13, 1906, p. 223.

§ See first paper.

*Summary.*

These experiments show that albinoes breed true to albinism, whether their ancestry is pigmented or not. They further show that, though externally albinoes may appear to be identical with regard to their coat characters, in reality they may be different. This fact has been previously known for both animals and plants, but it has hitherto been elucidated by means of breeding tests alone. These experiments add an ocular demonstration of the actual presence of the coat-pattern in albinoes. The interpretation placed upon the coat appearances in these albinoes is corroborated by the breeding results.

It is further shown that when a piebald black rat (Cr 5) is mated with a similar one, two classes of offspring may be obtained. One of these contains all black piebalds and the other a mixture of black piebalds and albinoes in nearly equal numbers.

When a piebald black rat is mated with an albino (=Cr. 5 × Cr 4), it may be said that, so far as these experiments have gone, five different results will be obtained. They may be stated as follows: (1) The offspring are all black piebalds. (2) They may be a mixture of black piebalds and albinoes. (3) They may be all "Irish" forms (=a black self-coloured form). (4) They may be a mixture of albinoes, black piebalds, and "Irish." (5) They may contain albinoes, "Irish," and a grey form (=Cr 2). It can be shown that the divergency of the results obtained when two individuals apparently similar are mated is due to the gametic nature of the albino employed.